

THE RELATIONSHIP BETWEEN SPOTTED OWL DIET AND REPRODUCTIVE SUCCESS IN THE SAN BERNARDINO MOUNTAINS, CALIFORNIA

RICHARD B. SMITH,^{1,2} M. ZACHARIAH PEERY,^{1,3,5} R. J. GUTIÉRREZ,¹ AND WILLIAM S. LAHAYE^{1,4}

ABSTRACT.—We analyzed the breeding season diets of California Spotted Owls (*Strix occidentalis occidentalis*) in the San Bernardino Mountains from 1987 through 1991 to estimate the relative importance of individual prey species to owl reproduction. We identified a total of 8441 prey remains from 109 unique territories, which represents the largest collection of prey remains from a single Spotted Owl population. Dusky-footed woodrats (*Neotoma fuscipes*) and Jerusalem crickets (*Stenopelmatus fuscus*) were the most frequently consumed taxa (42.2% and 20.7%, respectively), but dusky-footed woodrats dominated Spotted Owl diets by biomass (74.0%). Spotted owls consumed primarily mammals by both frequency (66.4%) and biomass (95.3%). After excluding territories with less than 20 prey remains, we compared the diets of 24 nonnesting, 24 unsuccessfully nesting, and 58 successfully nesting pairs of Spotted Owls from 56 unique territories; estimated diet along a large elevational gradient; and controlled for interterritorial and annual variation in diet. A significant relationship existed between reproductive status and the percent biomass of woodrats in Spotted Owl diets where successful nesters consumed a greater percent biomass of woodrats (\bar{x} = 81.8) than nonnesters (\bar{x} = 74.1) but not unsuccessful nesters (\bar{x} = 75.5). Unsuccessful nesters and nonnesters did not consume a significantly different percent biomass of woodrats. The percentage of woodrat biomass in Spotted Owl diets increased with elevation but did not differ among territories or years. We hypothesized that breeding Spotted Owls were able to meet the increased energetic demands associated with producing young by consuming primarily large, energetically profitable prey such as woodrats. Received 6 May 1998, accepted 21 Oct. 1998.

The Spotted Owl (*Strix occidentalis*) preys on a wide range of vertebrate and invertebrate taxa, but primarily on a few species of small mammals (Gutiérrez et al. 1995). The distribution of these small mammals has an important influence on the owl's home range size (Carey et al. 1992, Zabel et al. 1995), habitat use patterns (Carey et al. 1992, Carey and Peeler 1995, Zabel et al. 1995, Ward et al. 1998), and demographic rates (Franklin 1997, Ward et al. 1998). In particular, prey abundance positively influences Spotted Owl reproduction. Ward and coworkers (1998) found that dusky-footed woodrats (*Neotoma fuscipes*) were more abundant in the territories of breeding Northern Spotted Owls (*S. o. caurina*) than in the territories of nonbreeding owls. Although this difference was not statistically

significant, the authors suggested that high variation in woodrat abundances resulted in low statistical power for rejecting the hypothesis of no difference between breeders and nonbreeders. Franklin (1997) showed that the distribution of woodrat habitat explained a large amount of interterritorial variation in Northern Spotted Owl reproductive success. In addition, studies of other strigids demonstrate convincingly that reproduction for most owl species is limited, at least in part, by prey availability (see Verner et al. 1992 for a review).

Assuming that Spotted Owl reproductive success is determined in part by food availability, food habit studies based on prey remains from egested pellets can be used to examine the relative importance of individual prey species for reproduction. Such studies have shown that successful breeders consume a greater proportion of large prey than unsuccessful breeders (Barrows 1985, 1987; Thrailkill and Bias 1989; White 1996), although Ward and coworkers (1998) found no difference. These studies have been based upon relatively few prey items or owl territories which has resulted in (1) data being pooled among territories or (2) data from a

¹ Dept. of Wildlife, Humboldt State Univ., Arcata, CA 95521.

² Present Address: P.O. Box 266, Mattituck, NY 11952.

³ Present Address: 927 Lincoln Way, San Francisco, CA 94122.

⁴ Present Address: P.O. Box 523, Big Bear City, CA 92314.

⁵ Corresponding author; E-mail: mzp1@axe.humboldt.edu

particular territory being considered independent from year to year. The first approach weights all territories equally regardless of the number of prey items collected. For example, a breeding territory from which one prey item was collected is given the same weight as a breeding territory with hundreds of prey items. The second approach results in pseudoreplication and can dramatically inflate the probability of rejecting the null hypothesis (Hurlbert 1984) that breeding and nonbreeding Spotted Owls have the same diets. This is especially likely because Spotted Owl diets exhibit interterritorial variation (Laymon 1988).

Because previous diet studies were based on relatively few territories sampled from large, open populations, inferences about the relationship between diet patterns and the breeding ecology of the Spotted Owl are limited. We have been studying the entire population of California Spotted Owls (*S. o. occidentalis*) in the San Bernardino Mountains of southern California since 1987. It is the largest subpopulation within the southern California owl metapopulation (Noon and McKelvey 1992, LaHaye et al. 1994) and occupies a diverse array of habitats along a large elevation gradient. This allowed us to estimate diet over a range of ecological conditions and reliably evaluate its relationship with reproduction. In this paper we compare the diets of nonnesting, unsuccessfully nesting, and successfully nesting Spotted Owls throughout the breeding season (March through October), enumerate the food habits of individuals of this population, and compare our results to other food habit studies of the California Spotted Owl.

STUDY AREA AND METHODS

The San Bernardino Mountains Study Area was located approximately 140 km east of Los Angeles, California and encompassed 1890 km² with elevations ranging from 800–3500 m. Mean annual precipitation ranged from less than 20 cm to more than 100 cm and was strongly influenced by elevation and topography (Minnich 1988). The vegetation was diverse, ranging from Mojave Desert scrub (Vasek and Barbour 1988) at lower elevations to alpine (Major and Taylor 1988) on San Geronio Mountain. Most Spotted Owls occupied conifer dominated forest (Sawyer et al. 1988, Thorne 1988) between 1000 m and 2500 m elevation.

Owl survey methods.—We surveyed the study area for Spotted Owls following methods described by Franklin and coworkers (1996) during the breeding

season (March–October), 1987–1991. We conducted 1113 nocturnal surveys during which we spent 15 min at an individual point or walked along designated routes, using vocal imitations of Spotted Owl calls to survey the forested habitat within the study area. Survey points and routes were placed so that all of this potentially suitable habitat was surveyed each year. We conducted 1659 diurnal surveys at territories that were known to be occupied in order to locate nests, locate roosts, collect regurgitated pellets, and assess reproductive status. We conducted initial diurnal surveys for each territory in March or April and conducted follow-up diurnal surveys every 3 to 5 weeks. We collected pellets by thoroughly searching areas underneath Spotted Owl nests and roosts during most diurnal surveys. We assessed nesting status by feeding owls live mice (*Mus musculus*) during diurnal surveys (Franklin et al. 1996). We considered an owl pair not to have nested if one member of the pair ate or cached four consecutive mice during a single diurnal survey prior to 31 May. Although only one formal survey was conducted to assess nesting status, multiple surveys were conducted at each territory to band and resight owls. If a nest was located during one of these surveys, the owls at that particular territory were of course considered to be nesting. When a nest was located, we used the same method to locate fledglings or to determine nest failure. Owls that did not take sufficient mice were not included in the study.

Quantifying Spotted Owl diets.—We dissected all collected pellets and isolated all identifiable prey remains. Identifiable remains included skulls (birds and mammals), mandibles (mammals, reptiles, and invertebrates), legs (birds and invertebrates), claws (invertebrates), and bills (birds). Remains collected during each diurnal survey were enumerated to the lowest possible taxonomic level, and the highest count was taken as the total number of prey items for that survey. If, for example, pellets collected during a single survey contained one woodrat skull, two left mandibles, and three right mandibles, three woodrats were considered to be present. The percent frequency of each taxa (Marti 1987) was then calculated for each territory pooled among years. The percent biomass (Marti 1987) was calculated for each territory using the mean prey weights in Table 1. The mean percent frequency and biomass among territories were used as estimates of the overall diet composition. This approach weights all territories equally so that overall percentages were not biased towards territories with many prey remains (Swanson et al. 1974).

Statistical analyses.—Statistical analyses were performed only on the biomass data 1988–1991 because of small sample sizes in 1987 and because we felt biomass more accurately represented the energetic importance of each prey taxa.

We used a mixed-model ANOVA approach (Proc MIXED of pc SAS, version 6.12; Littell et al. 1996) to estimate variation in Spotted Owl diet, where each diet variable was considered as the dependent variable in a separate model. We treated reproductive status (non-

TABLE 1. Diet of Spotted Owls in the San Bernardino Mountains, California.

	Mean prey weight (g)	Source ^a	% of prey by frequency (n = 8,169)	% of prey by biomass (707,193 g)
Mammals				
<i>Neotoma fuscipes</i>	173.7	1	42.2	74.0
<i>Thomomys bottae</i>	124.4	1	7.4	10.4
<i>Glaucomys sabrinus</i>	121.5	2	2.1	3.0
<i>Peromyscus</i> spp.	22.1	1	11.3	4.0
<i>Microtus</i> spp.	60.2	1,2	1.8	1.3
<i>Sylvilagus</i> spp.	538.3	2	0.2	1.0
<i>Sciurus griseus</i>	785.0	2	0.1	1.0
<i>Dipodomys merriami</i>	42.1	2	0.1	<0.1
<i>Scapanus latimanus</i>	55.2	2	0.4	0.3
<i>Spermophilus lateralis</i>	153.4	1	0.1	0.2
<i>Tamius merriami</i>	67.6	1,2	0.1	0.1
<i>Antrozous pallidus</i>	21.5	2	<0.1	<0.1
<i>Eptesicus fuscus</i>	14.0	2	<0.1	<0.1
<i>Lasiurus cinereus</i>	25.5	2	0.1	<0.1
<i>Myotis</i> spp.	4.9	2	0.1	<0.1
<i>Perognathus</i> spp.	14.4	1	0.1	<0.1
<i>Sorex ornatus</i>	5.1	2	0.5	<0.1
Subtotal			66.4	95.3
Birds	64.4	3	4.3	3.5
Invertebrates				
<i>Stenopelmatus fuscus</i>	2.0	4	20.7	0.9
<i>Prionus californicus</i>	2.0	3	3.6	0.1
<i>Scorpionida</i>	2.0	4	2.7	0.1
Unidentified	2.0	4	2.1	0.1
Subtotal			29.1	1.2
Reptiles				
<i>Sceloporus</i> spp.	10.0	3	0.1	<0.1

^a Sources were (1) specimens from the San Bernardino Mountains in the Museum of Vertebrate Zoology at University of California, Berkeley collections, (2) specimens from nearest available location to the San Bernardino Mountains in the Museum of Vertebrate Zoology at University of California, Berkeley collections, (3) Forsman et al. (1984; biomass of birds divided by the number of birds in tables 12–14), (4) estimated based on prey size.

nesters, unsuccessful nesters, and successful nesters) and year as fixed effects, and elevation (at the center of activity for each territory) as a covariate. We used territory as a random blocking factor to estimate variation in diet among territories and control for non-independence of samples within territories. Two-way interactions between reproductive status and the other main effects were included in the model. Main effect by territory interactions were assumed to be nonexistent which resulted in all effects being tested over the residual mean square (Newman et al. 1997). Significant fixed effects were further tested with *t*-tests on least squares means using sequential Bonferonni adjustments on critical values (Rice 1989). This procedure involves testing each comparison, starting with the most significant and stopping at the first nonsignificant comparison, using $\alpha/(1 + k - i)$ as the critical value where *k* is the number of post-hoc comparisons and *i* is the number of the comparison.

Proper use of an ANOVA model requires a normally distributed dependent variable and equality of variances among treatment levels (Zar 1984). Because the percent biomass of woodrats was a proportional variable,

and hence formed a binomial distribution, we used the square root-aresine transformation to normalize the data (Zar 1984). Normality was then tested with the Shapiro-Wilk statistic (Zar 1984). Equality of variances among reproductive groups was tested with an *F*-test (Zar 1984).

By using diet as the dependent variable we do not imply that diet is a function of reproductive status; the mixed modeling approach simply provides a convenient way of examining variation in diet in relation to other variables (including reproduction). We believe that this approach is justified because (1) the goal of the study was to determine if diet differed among non-nesting, unsuccessfully nesting, and successfully nesting Spotted Owls, and (2) it is appropriate to analyze a correlative relationship with a linear model because the resultant *F*-statistic provides a test of the null hypothesis that the multiple correlation coefficient *R* is zero (Zar 1984).

RESULTS

Spotted Owl diets.—We identified a total of 8441 prey items from 109 unique Spotted Owl

TABLE 2. The effect of reproductive status, elevation, and year on the percent biomass of woodrats in Spotted Owl diets in the San Bernardino Mountains. Results are from a mixed-model ANOVA (Littel et al. 1996) where reproductive status and year were fixed effects, elevation was a covariate, and territory^a was a random blocking factor effect.

Effect	ndf	ddf	F	P
Reproductive status	2	36	3.65	0.04
Elevation	1	36	34.93	<0.01
Year	3	36	1.87	0.15
Reproductive status*year	3	36	1.17	0.35
Reproductive status*elevation	1	36	3.16	0.06

^a Territory was not significant ($Z = 1.43$, $P = 0.15$).

territories. This represents, to the best of our knowledge, the largest collection of prey items recorded from a single Spotted Owl population. When estimating the overall diet composition, we excluded territories from which fewer than 20 prey remains were collected during the entire study period (this resulted in a subsample of 8,169 prey remains from 71 territories). Dusky-footed woodrats and Jerusalem crickets (*Stenopelmatus fuscus*) were the most common taxa by frequency (42.2% and 20.7%, respectively). White-footed mice (*Peromyscus* spp.) and northern pocket gophers (*Thomomys bottae*) were less common by frequency (11.3% and 7.4%, respectively). No other taxa contributed more than 4.3% to the total number of prey items (Table 1).

Dusky-footed woodrats dominated Spotted Owl diet by biomass (74.0%), followed by pocket gophers (10.4%). Dusky-footed woodrats were the largest (173.7 g) of the common prey items. Western grey squirrels (*Sciurus griseus*) and cottontails (*Sylvilagus* spp.) were larger, but represented only 2.0% of the total biomass. No other taxa contributed more than 4.0% to the total biomass consumed (Table 1). Mammals contributed 66.4% and 95.3% to the total number of prey items and the total biomass, respectively. Invertebrates contributed 29.1% to the total number of prey items, but only 1.2% to the total biomass.

Variation in Spotted Owl diets.—For statistical analyses, we excluded territories represented by fewer than 20 prey items in any one year. In doing so, we retained a large sample size (106 samples from 56 unique Spotted Owl territories; 24 nonnesters, 24 unsuccessful nesters, and 58 successful nesters) and were able to estimate the percent biomass of

woodrats with reasonable precision on a territory by territory basis (mean CV = 0.08, maximum CV = 0.27). The percent biomass of pocket gophers was estimated with considerably less precision (mean CV = 0.50, maximum CV = 1.00). In addition, the percent biomass of pocket gophers was highly and negatively correlated with the percent biomass of woodrats ($r = -0.67$, $P < 0.01$, $n = 106$). For these reasons, we did not model the percent biomass of pocket gophers statistically.

Although the percent biomass of woodrats was not distributed normally ($W = 0.93$, $P < 0.01$) the variance in the percent biomass of woodrats did not differ between the least variable (successful nesters) and the most variable (unsuccessful nesters) reproductive groups ($F_{23,57} = 1.46$, $P > 0.05$). Because ANOVA is sensitive to heterogeneity of variances among treatment levels but robust to departures from normality (Hicks 1993), we assumed the data met the assumptions of the model.

A significant relationship existed between reproductive status and the percent biomass of woodrats in Spotted Owl diets (Table 2). Successful nesters consumed a greater percent biomass of woodrats ($\bar{x} = 81.8 \pm 1.5$ SE) than nonnesters ($\bar{x} = 74.1 \pm 2.4$; $t_{0.017,36} = 2.49$, $P = 0.017$) but not unsuccessful nesters ($\bar{x} = 75.5 \pm 2.4$; $t_{0.025,36} = 2.08$, $P = 0.044$), although the difference between successful and unsuccessful nesters was nearly significant. Unsuccessful nesters and nonnesters did not consume a different percent biomass of woodrats ($t_{0.050,36} = 0.04$, $P > 0.05$). The percentage of woodrat biomass in Spotted Owl diets did not differ among territories but increased with elevation (Table 2; Fig. 1). The interaction between elevation and reproductive status was

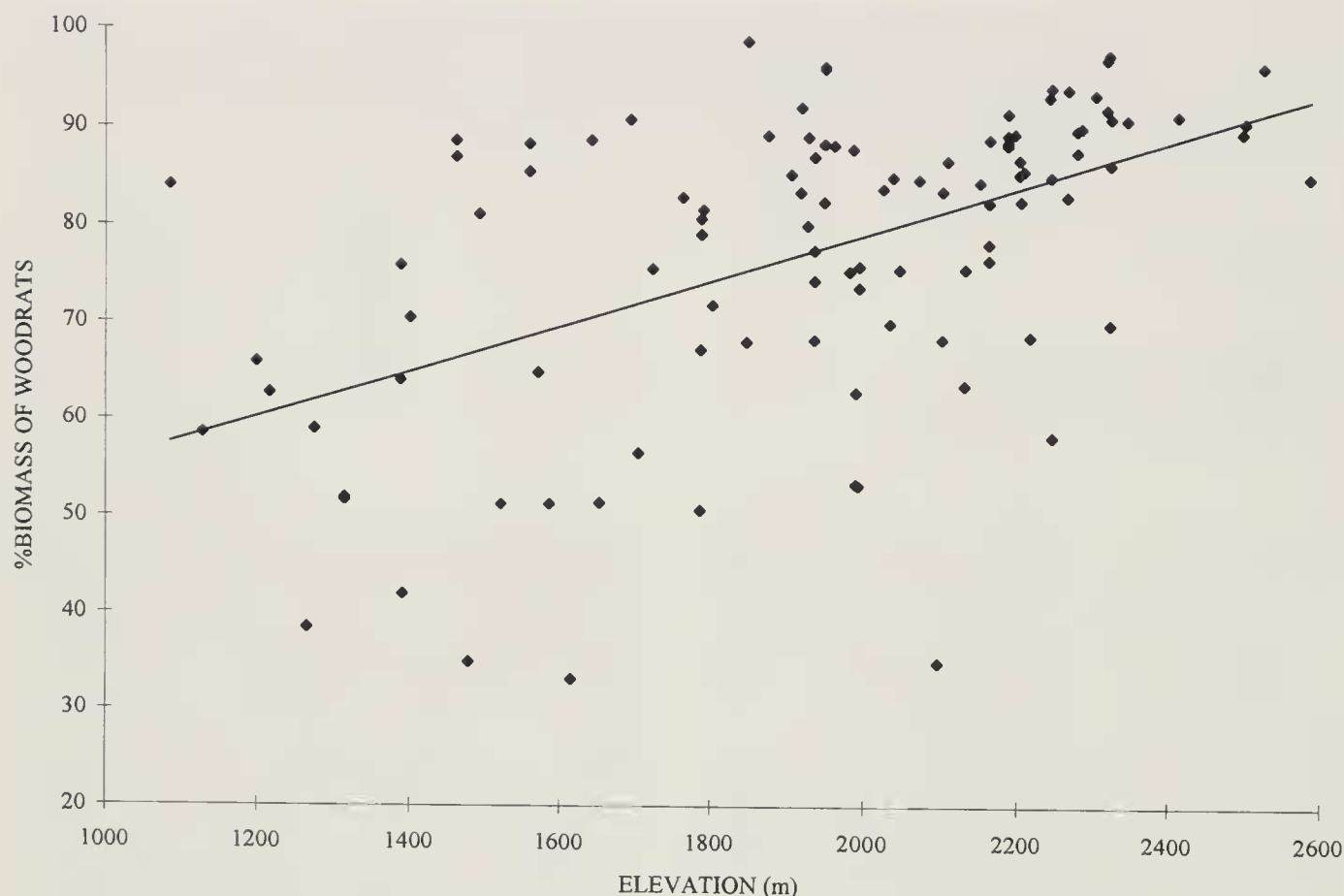


FIG. 1. The relationship between elevation and the percent biomass of woodrats in the diets of Spotted Owls in the San Bernardino Mountains, California, 1988–1991 ($b = 0.000085$, $R^2 = 0.26$, $df = 104$, $P < 0.01$).

not significant (Table 2), indicating that the percent biomass of woodrats increased with elevation at a constant rate for nonnesters, unsuccessful nesters, and successful nesters. The percentage of woodrat biomass in the owl's diet did not differ among years and no interaction existed between year and reproductive status (Table 2).

DISCUSSION

For an owl pair to produce young, females must acquire sufficient fat reserves prior to nesting, and males need to provide sufficient amounts of food to the female and nestlings during the nesting period (Hirons 1985). Dusky-footed woodrats are relatively large and may have provided an energetically profitable food source that enabled Spotted Owls to reproduce successfully. This idea is supported by Ward and coworkers (1998) who showed that selection of dusky-footed woodrats provided an indirect benefit to Spotted Owl fitness by reducing the amount of habitat needed to reproduce successfully. Further, Orrians and Pearson (1979) predict that central

place foragers such as Spotted Owls (Carey and Peeler 1995) can increase the rate of energy return to the central place (nest), and hence fitness, by consuming large prey. By consuming large prey, the male can minimize the number of flights from the point of capture to the nest, allowing more time for hunting.

Since the diet of unsuccessful nesters was more similar to nonnesters than successful nesters, consuming woodrats may be more important for incubation and brooding than for nest initiation. This is supported by the fact that the energetic cost of egg production is relatively small compared to the amount of energy needed to provision the female and young during the nesting period (Ward et al. 1998).

Our results support Barrows (1985, 1987), Thrailkill and Bias (1989), and White (1996) who found that Spotted Owls that fledged young consumed a higher proportion of large prey than Spotted Owls that did not fledge young. Despite the sample size limitations of these previous studies, it appears that a true difference in diet, particularly in terms of prey

size, exists between breeding and nonbreeding Spotted Owls. The importance of prey size has also been observed for Black-shouldered Kite (*Elanus caeruleus*; Slotow and Perrin 1992) and Common Kestrel (*Falco tinnunculus*; Korpimäki 1986) reproduction, suggesting that this may be a common pattern for raptorial species.

It is possible that the difference between successful nesters and nonnesters was statistically significant, but not biologically significant. An 8% difference in the percent biomass of woodrats is relatively small when compared to the additional amount of food a male must procure to provision a female and even just one nestling. Based upon Ward's and coworkers' (1998) energetic calculations, a male must increase the amount of food he procures by 276% in order to provision the female and a juvenile from egg-laying to fledging. However, the dietary difference observed between breeders and nonbreeders may be only one of the factors that allows an owl pair to produce young. For example, the variation in diet caused by breeding status may simply reflect higher prey availabilities in the territories of breeding and nonbreeding owls (see below).

The percent biomasses of the prey species presented here are not necessarily estimates of the total amount of prey taken because it is unlikely that we collected all regurgitated pellets. Hence we cannot evaluate the effect of food supply on reproduction. It is possible that even though successfully nesting owls consumed a greater percent biomass of woodrats, they obtained less total biomass from woodrats than nonnesters or unsuccessful nesters. However, this seems unlikely because breeding Spotted Owls need to take considerably more total prey to feed their juveniles.

Without measuring prey abundances, we cannot be certain if the relationship between Spotted Owl diet and reproduction was the result of differences in prey availability or prey selection among territories. Spotted Owls select dusky-footed woodrats more than would be expected based on availability in both northern and southern California (Hedlund 1996, Ward et al. 1998). Further, Barrows (1987) found that Spotted Owl pairs shift from large to small prey after nest failure and suggested that this change in prey selection was

in response to reduced energy requirements. If Barrow's hypothesis was true for our population, unsuccessful nesters should have had an intermediate percentage of woodrat biomass in their diets. Since this did not occur, we consider it more likely that the difference in the percent biomass of woodrats between owls that fledged young and owls that did not fledge young was the result of differences in prey availability among territories. Optimal foraging theory (see Pyke et al. 1977 for a review) predicts, and raptor field studies show (Korpimäki 1986, Steenhof and Kochert 1988), that when the density of primary prey is high within the landscape, the percentage of that prey in the predator's diet is also high (i.e., a functional response). Hence, if woodrats occurred at higher densities in the territories of successfully reproducing owls (Franklin 1997, Ward et al. 1998) one would expect these owls to consume a greater percentage of woodrats.

Bull and coworkers (1989) found that male Great Gray Owls (*S. nebulosa*) preferentially consumed small prey items at the point of capture and brought large prey items back to the nest. Although this presents a potential source of bias, we do not believe that it affects the conclusions of this study. For nesting owls, our pellets were probably biased towards males because we (1) often located male roosts and (2) females frequently flew away from the nest to egest pellets (personal observation). If Bull's and coworkers' (1989) findings are true for Spotted Owls, we may have underestimated the percent biomass of woodrats in the diets of nesting owls. This bias, however, would have decreased the difference between owls that fledged young and owls that did not fledge young.

Another potential bias is that pellets may not represent a random sample of the owl's diet. In particular, single prey-item Barn Owl (*Tyto alba*) pellets are more likely to contain large prey than expected by chance (Yom-Tov and Wool 1997). If this was true for our Spotted Owl population, the percent frequency and biomass of relatively large prey such as woodrats, pocket gophers, and northern flying squirrels (*Glaucomys sabrinus*) would be positively biased, while the percent frequency and biomass of relatively small prey such as white-footed mice would be negatively bi-

ased. However, these biases should be consistent for nonnesting, unsuccessfully nesting, and successfully nesting owls and should not affect the relationship between reproductive status and diet that we observed.

Although some similarities existed between Spotted Owl diets in the San Bernardino Mountains and other localities in southern California, some marked differences existed as well. For example, while the percent frequencies of woodrats and pocket gophers in Spotted Owl diets reported in this study were similar to those reported by Barrows (1980, 1987), white-footed mice comprised a considerably smaller percentage (11.3% versus 40.0%) and invertebrates a greater percentage (29.1% versus 18.0%) of the total prey items in this study. The percent biomasses of woodrats, pocket gophers, and most other prey taxa were remarkably similar to those reported by Barrows (1980, 1987).

In the Sierra Nevada, woodrats are the Spotted Owl's primary prey at low elevations but are almost completely replaced by flying squirrels at high elevations (Verner et al. 1992). In the San Bernardino Mountains, woodrats increased in Spotted Owl diets with elevation and flying squirrels were uncommon (2.1%). Flying squirrels are probably more abundant in the upper mixed-conifer and red fir (*Abies magnifica*) zones of the Sierra Nevada (see Waters and Zabel 1995) than they are in the San Bernardino Mountains where they reach the southern edge of their range (Hall and Kelson 1959). The San Bernardino Mountains apparently lack a relatively large alternative prey species at higher elevations and it is possible that most of the other prey species decrease in elevation as well. Woodrats are an important part of the Spotted Owl's diet in southern California, both in terms of biomass and reproduction, and we recommend that future management of forested habitat in this region promote high woodrat densities.

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